Influence of urbanization on the epidemiology of intestinal helminths of the red fox (Vulpes vulpes) in Geneva, Switzerland

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ORIGINAL PAPER

Influence of urbanization on the epidemiology of intestinal helminths of the red fox (*Vulpes vulpes*) in Geneva, Switzerland

Leslie A. Reperant · Daniel Hegglin · Claude Fischer · Lucia Kohler · Jean-Marc Weber · Peter Deplazes

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Abstract Dixenous helminths that depend on rodent intermediate hosts are supposed to be negatively affected by urbanization due to lower supply of rodents in urbanized environments. Prevalence rates of dixenous, non-strictly monoxenous, and monoxenous helminths in 228 red foxes (*Vulpes vulpes*) along a gradient of increasing urbanization were assessed by morphological parasite identification in the city of Geneva, Switzerland. Multivariate analyses for the five most prevalent helminth species or genera revealed a significant decrease of prevalence rates for the dixenous helminths *Echinococcus multilocularis* and *Taenia* spp. from the rural (52.1 and 54.3%, respectively) to the urban area (30.0 and 20.0%, respectively), but not for the monoxenous nematode *Uncinaria stenocephala* (overall prevalence of 78.2%) and the non-strictly monoxenous nematode *Toxocara canis* (overall prevalence of 44.3%). The lower prevalence of *Toxascaris leonina* in the urban area (8.0%) compared to the rural area (59.6%) raises the question of whether rodent paratenic hosts play a major role for the population dynamics of this species.

L. A. Reperant · D. Hegglin · L. Kohler · P. Deplazes (✉)
Institute of Parasitology, University of Zurich,
Winterthurerstrasse 266a,
CH-8057 Zurich, Switzerland
e-mail: deplazesp@access.uzh.ch

Present address:
L. A. Reperant
Department of Ecology and Evolutionary Biology,
Princeton University,
Princeton, NJ 08544-1003, USA

C. Fischer
Department of Ecology and Evolution, University of Lausanne,
Bâtiment de Biologie,
CH-1015 Lausanne, Switzerland

J.-M. Weber
KORA (Co-ordinated Carnivore Research Projects),
Thunstrasse 31,
CH-3074 Muri, Switzerland

Introduction

A dramatic increase in red fox populations (*Vulpes vulpes*) has been reported throughout Europe, especially in urban areas. In Switzerland, the increase of urban fox populations started in the mid-eighties and coincided with the end of the rabies epizootic (Gloor et al. 2001). The red fox is host of a number of canine helminths, including the zoonotic parasites *Echinococcus multilocularis* and *Toxocara canis*. The so-called city-fox phenomenon and, thereafter, the increased proximity of foxes with humans and domestic dogs may, therefore, have significant public health implications (Deplazes et al. 2004).

The small-fox tapeworm, *E. multilocularis*, is one of the most pathogenic zoonotic parasites in Europe, leading to alveolar echinococcosis in humans (Eckert and Deplazes 2004). In Europe, natural intermediate hosts of *E. multilocularis* include arvicolid rodents of open habitat, notably the water vole (*Arvicola terrestris*) and the common vole (*Microtus arvalis*). The red fox is referred to as the primary definitive host of *E. multilocularis* and responsible for the contamination of the intermediate host habitat, disseminating eggs with the feces (Eckert and Deplazes 2004).

Toxocara canis is an intestinal ascarid frequently found in dogs and red foxes in Europe. Although directly transmitted, adult canids can also acquire intestinal infection after the ingestion of infected paratenic hosts. These are mostly rodents, but also birds and invertebrates (Despommier 2003). Human toxocarosis is a zoonosis caused by migrating tissue larvae of *Toxocara* spp., which can be potentially severe especially in children (Overgaauw 1997; Magnaval et al. 1998; Despommier 2003). Domestic carnivores contaminating the environment with their feces are assumed to be the primary sources of infections for humans. However, red foxes could play another significant role in the transmission of this zoonosis (Richards et al. 1993; Epe et al. 1999; Richards and Lewis 2001).

The red fox is a generalist predator, feeding mostly on small mammalian prey, birds, invertebrates, and fruit. However, in rural central Europe, the majority of its diet is composed of Arvicolid rodents from open habitat and, notably, *A. terrestris* and *Microtus* spp. (Artois et al. 1989; Weber and Aubry 1993; Ferrari and Weber 1995). Due to substantial and distinct food resources occurring in urban environments, the diet of urban foxes differs from the diet of their rural conspecifics. It comprises a higher proportion of anthropogenic food and invertebrates and a lower occurrence of mammalian prey (Doncaster et al. 1990; Contesse et al. 2004). Further, because of a constant high availability of anthropogenic food resources, specific social structures and smaller home ranges are observed within cities, leading to higher fox densities than in rural settings (Harris and Rayner 1986). The consequences of urbanization on the ecology of red foxes are, thus, likely to result in noticeable effects on the population dynamics of different fox parasites.

Dixenous helminths such as *E. multilocularis* and other taeniid species rely on predator–prey relationships for the completion of their life cycles. As the level of urbanization affects the predation rate of foxes upon rodents and, in particular, upon Arvicolid prey (Hegglin et al. 2007), a decrease in the prevalence of these dixenous helminths in foxes is expected in urbanized environments. If rodent paratenic hosts have a significant impact on the population dynamics of a non-strictly monoxenous helminth, a similar effect of urbanization on prevalence rates can be expected as for dixenous helminths. However, the role of paratenic hosts in the epidemiology of helminths, notably ascarids, remains poorly understood. In contrast, transmission of monoxenous helminths, such as the hookworm *Uncinaria stenocephala*, is mainly dependent upon the abundance and survival of the free-living stages, and host density (Arneberg et al. 1998). Accordingly, and assuming no significant decrease in the survival rate of their free-living stages with the increase of urbanization, a steady prevalence of monoxenous helminths in foxes is anticipated.

In this study, the prevalence patterns of non-strictly monoxenous, monoxenous, and dixenous intestinal helminths were compared along an urban gradient.

Materials and methods

Study area

The study was carried out in the canton of Geneva, Switzerland, a densely populated area of 240 km^2 with 400,000 inhabitants. Permanent grassland accounts for 19% of the canton and forests for less than 10%. Following Fischer et al. (2005), the study area was subdivided into three zones of increasing degree of urbanization related to human density. The categorization of zones was based on a grid of 100 m^2, and an adaptive Kernel method was used to smooth the shapes of the three areas. Fifty-one percent of the total area is rural with a human population density ranging from 0 to 40 inhabitants per km^2. Land use is mainly agricultural. The residential area surrounds the city of Geneva and the shores of the lake. It represents a thin belt of 26% of the total surface and is mostly constituted of individual housing with private gardens. Human population density ranges from 40 to 220 inhabitants per km^2. The urban area represents 23% of the total surface. Human population density reaches up to 3,790 inhabitants per km^2.

Sampling of red foxes

From 1998 to 2002, 228 red foxes collected from all parts of the canton of Geneva were analyzed parasitologically. Exact locations were recorded by global positioning system (GPS), and the foxes were frozen before necropsy. Mortality was mainly due to collision with vehicles (>75%). The age determination of the foxes was done by measuring the relative width of the pulp cavity of a lower canine tooth by X-rays (Kappeler 1991), discriminating adults (>1 year old) from juveniles. Juveniles counted for 103 animals and adults for 125. A total of 94 carcasses were collected in the rural area, 84 in the residential area and 50 in the urban area. No statistical difference in the age or sex ratio of red foxes was detected between the three urbanization zones.

Parasitological examination

Necropsy and examination of the intestines were carried out following strict safety precautions, and intestinal helminths were recovered by the intestinal sedimentation and counting technique (Hofer et al. 2000).

Species identification of isolated helminths specimens was based on morphological features of parasites. Because of the deep-freezing procedure of all intestines, specific morphological identification of large cestodes to the species level was not possible. Diagnoses to the genus level was achieved by microscopical identification of proglottids. The species identification of hookworms was based on the morphological shape of the bursa of males. As all males were identified as *U. stenocephala*, all females were considered to be from the same species. Ascarid species were identified by the morphological shape of the eggs (mature females) and of the dorsal lips (immature females and males; Mozgovoi 1968). If the individual worm burden of ascarids was >10 per fox, the species of ten randomly selected worms were identified. However, in 18 intestines that were randomly distributed in space and time, the ascarids could not be identified to the species level. As a consequence, the prevalence rates presented for ascarid species have to be considered as minimal prevalence rates.

Statistical analysis

Statistical analyses were performed with Statistical Package for the Social Sciences (SPSS)–PC version 13.0. Stepwise backward logistic regression (using likelihood ratio) was used to test the effect of year, season (winter, December to February; spring, March to May; summer, June to August; fall, September to November), urbanization zone, age class, and sex on the prevalence of the helminths. In the initial model, the 'age–season' interaction was included, as season-related differences might be closely associated with the age structure of the fox population. Results were considered significant when $P \leq 0.05$. Prevalences were reported with the exact binomial 95% confidence interval (CI) following Clopper and Pearson (1934).

Results

Recovered intestinal helminths

Nematodes were the most prevalent class recovered. A total of 92.6% foxes were infected with at least one of the four recovered intestinal nematode species (*U. stenocephala*, 78.2%; *Toxocara canis*, 44.3%; *Toxascaris leonina*, 37.3%; and *Trichuris vulpis*, 8.3%). No specimens of *Ancylostoma caninum* nor *Toxocara cati* were identified. *Toxocara canis* and *Toxascaris leonina* co-occurred in 14.0% of the fox intestines, and no association was detected neither in the whole data set nor in the subsamples of foxes from different zones or of different age class.

The cestodes *E. multilocularis* and *Taenia* spp. were prevalent (46.3 and 41.9%, respectively). *Mesocestoïdes* spp. (5.7%), *Dipylidium* spp. (2.2%), and a single specimen of *Diphyllobothrium* spp. were also recovered. Intestinal trematodes were present in 27 foxes (prevalence of 11.8%) but not further identified. For further multivariate analysis, helminths species or genera with prevalences above 20% were investigated.

Dixenous helminths

The stepwise backward logistic regression analyses produced two models for the occurrence of the dixenous helminths *E. multilocularis* and *Taenia* spp. in foxes (χ^2=7.0, df=4, p=0.135, and χ^2=25.1, df=6, p<0.0001, respectively; Table 1). The urbanization zone was the only

Table 1 Odd ratios and confidence intervals of the parameters included in the final models (stepwise backward logistic regressions) explaining the prevalence rates of the five main helminths recovered in 228 foxes from the canton of Geneva, Switzerland

Variables	Category/ref. category	*Uncinaria stenocephala*		*Toxascaris leonina*		*Toxocara canis*		*Echinococcus multilocularis*		*Taenia* spp.	
		OR	CI=95	OR	CI=95	OR	CI=95	OR	CI=95	OR	CI=95
Year		–		–		–		–		–	
Season	Winter/fall	6.526	1.25–34.03	–		–		–		–	
	Spring/fall	1.113	0.40–3.12	–		–		–		–	
	Summer/fall	0.561	0.15–2.15	–		–		–		–	
Age	Juveniles/adults	4.632	0.88–24.52	–		–		–		2.307	1.30–4.09
Sex	Male/female	–		–		–		–		–	
Urbanization zone	Rural/urban	–		16.95	5.63–50.99	–		2.541	1.23–5.26	5.431	2.38–12.41
	Residential/urban	–		4.89	1.58–14.99	–		2.225	1.06–4.67	2.643	1.15–6.07
Age×season	Juveniles×winter / adults×fall	0.061	0.01–0.68	–		0.98	0.42–2.28	–		–	
	Juveniles×spring/ adults×fall	0.123	0.02–0.96	–		4.57	1.39–15.03	–		–	
	Juveniles×summer/ adults×fall	0.694	0.08–5.90	–		3.07	1.45–6.50	–		–	

CI=95:95% confidence interval
OR Odd ratio

variable that had a significant effect on the prevalence of *E. multilocularis* (LR=6.6, *df*=2, *p*=0.037) and was as well included in the model explaining the variations in the prevalence of *Taenia* spp. (LR=16.0, *df*=2, *p*<0.0001). The prevalence of *E. multilocularis* and *Taenia* spp. decreased from 52.1% (CI=41.6–62.5%) and 54.3% (CI=43.7–64.6%), respectively, in the rural area to 48.8% (CI=38–60%) and 41.2% (CI=30–52%) in the residential area, to 30.0% (CI=17.9–44.6%) and 20.0% (CI=10.0–33.7%) in the urban area (Fig. 1a and b, respectively).

The age class had a significant effect on the prevalence of *Taenia* spp. (LR=7.8, *df*=1, *p*=0.005), but not on the prevalence of *E. multilocularis*. Juveniles were found more frequently infected than adults (prevalence of 50.5%, CI=40.5–60.5, and 34.4%, CI=26.1–43.4%, respectively).

Non-strictly monoxenous helminths

Significant models were found to explain the variations of the prevalence of *Toxocara canis* and *Toxascaris leonina* in foxes (χ^2=14.9, *df*=3, *p*<0.001, and χ^2=44.2, *df*=2, *p*<0.0001, respectively; Table 1). The interaction 'age–season' was included in the model explaining the variations of the prevalence of *Toxocara canis* (LR=13.8, *df*=3, *p*=0.003; Table 1). Whereas it remained stable in adult foxes along seasons (mean prevalence of 36.8%, CI=28.4–45.9%), it was highest in spring (prevalence of 73.3%, CI=44.9–92.2%) and decreased thereafter from summer (64.9%, CI=47.5–79.8%) to fall (41.7%, CI=22.1–63.4%) to remain at a similar lever during winter (40.0%, CI=21.1–61.3%) in juveniles (Fig. 2a).

The urbanization zone had a highly significant effect on the prevalence of *Toxascaris leonina* (LR=33.0, *df*=2, *p*<0.0001). The overall prevalence decreased from 59.6% (CI=49.0–69.6%) in the rural area to 29.8% (CI=20.3–40.7%) in the residential area, to 8.0% (CI=2.2%–19.2%) in the urban area (Fig. 1c). In contrast, prevalence of *Toxocara canis* remained stable along the three urbanization zones (39.4% in the rural, 46.4% in the residential, and 50.0% in the urban area).

Monoxenous helminth

The final model explaining the variations of prevalence of the strictly-monoxenous nematode *U. stenocephala* (χ^2=

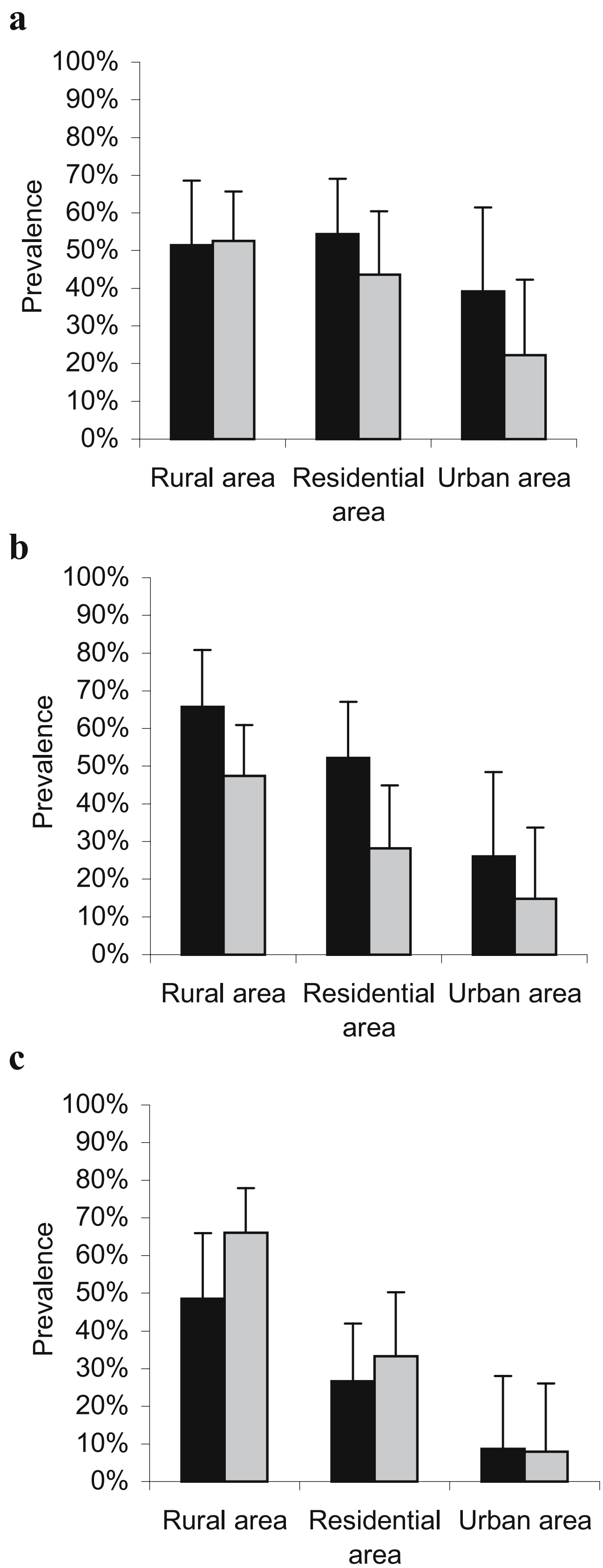

Fig. 1 Significant spatial variations of the prevalence of the dominant helminths of red foxes from Geneva, Switzerland, along an urban gradient. Juvenile foxes (*black bars*, *N*=103) and adult foxes (*gray bars*, *N*=125): **a** prevalence of *E. multilocularis*, **b** *Taenia* spp., and **c** *Toxascaris leonina*. *Whiskers* represent the upper exact 95% confidence interval

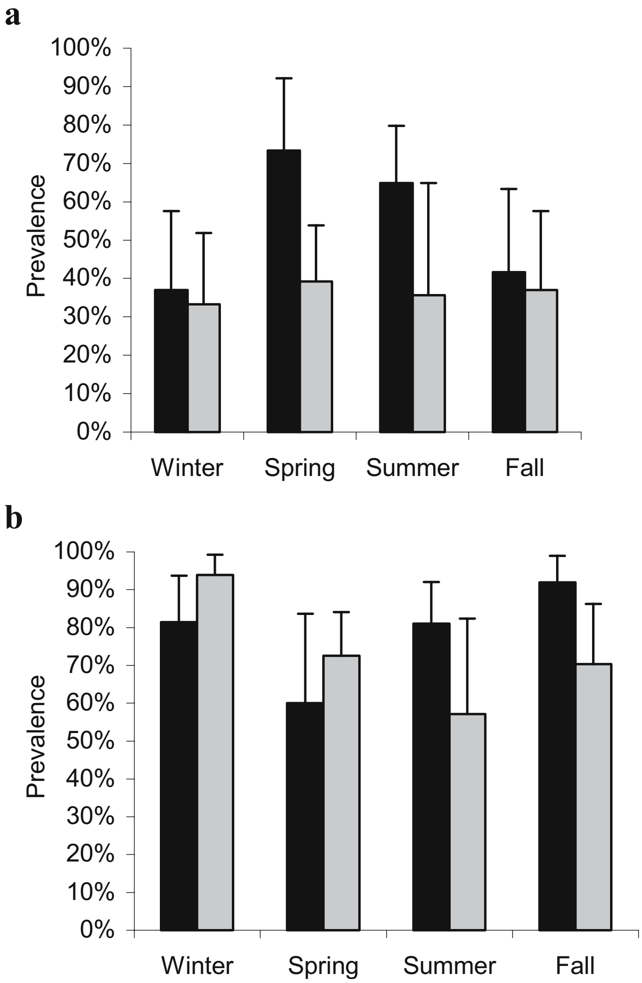

Fig. 2 Significant seasonal variations of the prevalence of the dominant helminths of red foxes from Geneva, Switzerland. Juvenile foxes (*black bars*) and adult foxes (*gray bars*): **a** prevalence of *Toxocara canis* and **b** *Uncinaria stenocephala*. *Whiskers* represent the upper exact 95% confidence interval

17.2, *df*=5, *p*=0.004) included the age (LR=3.9, *df*=1, *p*=0.048), the season (LR=10.9, *df*=3, *p*=0.012), and their interaction (LR=9.0, *df*=3, *p*=0.030) as significant variables (Table 1). The prevalence in juveniles was lowest in spring (60.0%, CI=32.3–83.7%) and highest in fall (91.7%, CI=73.0–99.0%), whereas the prevalence in adults was lowest in summer (57.1%, CI=28.9–82.3%) and highest in winter (93.9%, CI=79.8–99.3%; Fig. 2b). The final model revealed no significant effect of the urbanization zone on the prevalence of *U. stenocephala*.

Discussion

Spatial variations of prevalence rates are described for a wide range of intestinal helminth communities in urban and periurban foxes. Variations in the population densities of final, intermediate, and paratenic hosts in the parasites' transmission biology and in the survival probabilities of parasites' free living stages are likely to be major factors contributing to this phenomenon. Dixenous rodent-related helminths (e.g., taeniids) were found less prevalent in foxes in urbanized environments (Richards et al. 1993, 1995; Willingham et al. 1996; Hofer et al. 2000; Saeed et al. 2006). These results and our present study suggest that predation of foxes on rodent intermediate hosts in urban areas might be reduced or altered. This hypothesis is supported by the results of the stomach analyses demonstrating that foxes in urban areas do not only predate less on rodents, but that the rodent prey spectrum in rural and urban areas also differs significantly (Hegglin et al. 2007). Both a decrease in the urban foxes' predation rate and changes in the rodent community and its susceptibility to taeniid infections are likely to account for the observed decreasing prevalences of dixenous helminths. In contrast, the prevalence of the strictly monoxenous nematode *U. stenocephala* remained stable along the increasing gradient of urbanization. Contrary to dixenous helminths, the main route of infection of this hookworm is the ingestion of free-living third-stage larvae (Richards et al. 1995), and the completion of its life cycle does not require rodent hosts.

The population of foxes investigated was frequently infected with *Toxocara canis* and/or *Toxascaris leonina*, but no association was found between these two species. To the best of our knowledge, this situation appears unique as surveys usually report the dominance of one or the other species (Richards et al. 1995; Willingham et al. 1996; Gortazar et al. 1998; Criado-Fornelio et al. 2000; Hofer et al. 2000; Smith et al. 2003; Saeed et al. 2006). Both species are directly transmitted but can potentially infect paratenic hosts, including rodents (Despommier 2003). The prevalence of *Toxascaris leonina* decreased dramatically with the increase in the level of urbanization of the habitat. Only few data is available concerning the epidemiology of this species. Therefore, a possible role of rodent paratenic hosts in the population dynamics of *Toxascaris leonina* has to be confirmed with further studies. Unlike *Toxascaris leonina*, *Toxocara canis* can be transmitted to fetus in utero or to newborn canids via milk, and these are considered significant routes of infection in dogs (Burke and Roberson 1985a, b). High prevalence rates in juvenile foxes during spring and summer tend to indicate a similar situation in this species. Further, the prevalence of *Toxocara canis* in juveniles decreased from spring and summer to fall and winter to levels similar to those observed in adults along seasons. Accordingly, age-related differences were observed in domestic dogs (Luty 2001; Habluetzel et al. 2003) and in red foxes

(Richards et al. 1993; Willingham et al. 1996; Luty 2001; Saeed et al. 2006), with highest prevalence rates in animals of less than 6 months of age. In adult canids, massive ingestion of infective *Toxocara canis* eggs result in somatic infections, only involving migrating larvae in various organs and tissues. In contrast, the ingestion of low numbers of embryonated eggs or the ingestion of infected paratenic hosts leads to intestinal infections (Magnaval et al. 1998; Saeed et al. 2005). Our results demonstrate a constant intestinal infection rate in adult foxes along seasons and along urbanization zones, suggesting either a constant but low infection pressure (ingestion of low numbers of infective eggs or ingestion of paratenic hosts) or a steady recruitment of somatic larvae in the maintenance of intestinal infections.

Both *E. multilocularis* and *Toxocara canis* occur in urban foxes in Geneva, emphasizing a particular zoonotic risk. However, in Geneva, not only the prevalence but also the abundance of *E. multilocularis* in foxes decreased from rural and residential areas to the city center, suggesting a lower infection pressure in the most urbanized part of the city (Fischer et al. 2005). Therefore, the residential or periurban area, at the interface of the rural and urban areas, represents the habitat of main exposure risk to *E. multilocularis* for humans, as it is intensely used by foxes, people, and domestic carnivores (Deplazes et al. 2004). On the other hand, no significant influence of the degree of urbanization of the habitat was detected on the prevalence of *Toxocara canis*. Soil contamination by *Toxocara* eggs has been found higher in urban than in rural or periurban areas (Mizgajska 1997; Giacometti et al. 2000; Mizgajska 2001). The high contamination of urban environment is thought to result from a higher density of domestic carnivores, particularly in urban parks and green areas (Mizgajska 1997). However, we demonstrated high prevalence rates of *Toxocara canis* in both juvenile and adult red foxes in all areas investigated, indicating a non-negligible role of the fox as a reservoir of *Toxocara canis*.

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